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The limits of modifying migration speed to adjust to climate change

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One Sentence Summary: Modifying migration speed does not allow sufficient adjustment of spring arrival in response to climate change in migratory birds.

Introductory paragraph

Predicting the range of variation over which organisms can adjust to environmental change is a major challenge in ecology[1,2]. This is exemplified in migratory birds which experience changes in different habitats throughout the annual cycle[3]. Earlier studies showed European population trends declining strongest in migrant species with least adjustment in spring arrival time[4,5]. Thus, the increasing mismatches with other trophic levels in seasonal breeding areas[6,7] likely contribute to their large-scale decline. Here we quantify the potential range of adjusting spring arrival dates through modifying migration speeds by reviewing 49 tracking studies. Among individual variation in migration speed was mainly determined by the relatively short stop-over duration. Assuming this population response reflects individual phenotypic plasticity, we calculated the potential for phenotypic plasticity to speed-up migration by reducing stop-over duration. Even a 50% reduction would lead to a mere two day advance in arrival, considering adjustments on the final 2,000 km of the spring journey. Hence, in contrast to previous studies[8-10], flexibility in the major determinant of migration duration seems insufficient to adjust to ongoing climate change, and is unlikely to explain some of the observed arrival advancements in long-distance migrants.

Main Text: Human induced environmental change affects populations of most organisms on the globe[1]. Some species cope well with these changes, but many have struggled to adjust, resulting in rapid population declines[11,12]. It has seldom been demonstrated over which range of environmental change a species group can flexibly adjust, and the different mechanisms of adjustment (such as phenotypic plasticity and evolutionary change) involved usually remain obscure. An assessment of adjustment range is important, because it defines the operating space of environmental change without biodiversity loss. Here we aim to define the potential range of phenotypic adjustment in migration speed of long-distance migrant birds in response to climate change.

Each spring, billions of birds migrate from (sub-)tropical wintering grounds to their breeding areas. At their wintering grounds birds have little information on the progress of spring at their distant breeding areas, but arriving too early or too late is costly[13]. Evolution has equipped migratory birds with endogenous timing mechanisms enabling them to arrive at their migratory destinations on average at the optimal time[14]. Climate change alters this optimal time via the advance of spring. Migrant birds have partly responded by arriving at their breeding sites significantly earlier[1,5,15], but responses have typically been insufficient, resulting in a phenological mismatch with the primary food source at the breeding area[7]. Whether a mismatch affects population trends depends on the seasonality of habitats used, and evidence shows that a phenological mismatch (caused by insufficient advancement of breeding area arrival, and/or failure to reduce the interval between arrival and laying) can contribute (among other causes) to large-scale population declines[4,5,7,11,12], especially in long-distance migratory birds. Most evidence strongly suggests that individual migrants advance their spring arrival by a phenotypic response in the duration of migration, with mean population arrival being earlier when conditions are beneficial at the wintering grounds or along the migration route[8-10]. The central question in this paper is whether we can predict to what degree a reduction in migration time allows adjustment of breeding area arrival in

response to ongoing climate change, and when further advancement in spring arrival would need other mechanisms, such as evolutionary change[15].

Each migratory journey is characterized by a sequence of fuel storage at the departure or stop-over sites, and migratory flights to the next stop-over or destination site[16]. The total speed of migration is the distance travelled divided by the flight plus stop-over duration, and shows a wide phenotypic plasticity, varying between and within species[13]. As the rate of accumulating energy at stop-over is lower than the rate of energy expenditure in flight[16], the time required to complete migration is mainly determined by stop-over duration and less by travel speed[17]. Optimal migration theory is based on this premise[16], but how total stop-over duration quantitatively affects total speed of migration has never been generally assessed across multiple study systems. This is an essential step to assess the role of phenotypic flexibility in adjustment to spatio-temporal changes in the environment. Recent advances in miniaturized tracking devices, which precisely record bird movements, now allow assessment of the dependency of the speed of migration on total stop-over duration. Inferences about phenotypic plasticity ideally would be drawn from tracking individuals over multiple years. However, the paucity of these data[18] and the knowledge that stop-over duration of individuals depends on environments encountered[19] makes between-individual comparisons the most suitable approach for estimating the potential degree of plasticity. We envision this potential plasticity in energy accumulation rates in response to food availability, leading to shorter stop-over duration to replenish reserves for the next flight bout, if food is more abundant. As food availability in temperate and arctic regions often is positively related to temperature, we expect climate change to result in shorter stop-over periods. This approach enabled us to model how much individual birds could potentially advance spring arrival date by shortening their stop-overs.

Based on 49 tracking studies of 46 bird species including 320 individuals on spring migration (Supplementary Tables S1, S2), we show that 66% of variation in total migration

speed was explained by total stop-over duration and bird group (linear mixed effect model of total speed of migration, with explanatory variables: total stop-over duration, bird group, their two-way interaction, and field study as a random factor in a Bayesian approach, Methods, Supplementary Tables S3). We considered a stop-over as a more than one day stay at the same location. Note that tracks without stop-over days (Fig. 1a) do not necessarily mean non-stop migration, but rather continuous migration (e.g. nocturnal migration and diurnal resting/foraging). For these studies, average migration distance was 6,128 km (25th quantile: 3,0954 km; 75th quantile: 7,578 km), and species were pooled into seven taxonomic bird groups, i.e., geese ($n_{individuals}$=57), storks ($n_{individuals}$ =12), raptors ($n_{individuals}$ =21), waders ($n_{individuals}$ =69), gulls ($n_{individuals}$ =30), swifts ($n_{individuals}$ =17), and songbirds ($n_{individuals}$ =114; Supplementary Table S1).

As long predicted by optimal migration theory[16], we quantify here its major assumption: Total speed of migration was mostly affected by total stop-over duration, with a negative slope (Fig. 1a,c). The slopes describing the effect of stop-over duration on migration speed were of similar magnitude across six taxonomic bird groups (Fig. 1c), except in geese, where the effect was stronger. The generality of the pattern among diverse taxonomic groups suggests that the general biological mechanism of regulating total speed of migration is by variation in stop-over duration.

That flexibility in arrival dates at the breeding area results from variation in total stop-over duration is well illustrated for two migratory songbirds during an exceptionally late spring arrival in 2011; as a consequence of a drought at their eastern African stop-over site, they doubled their total stop-over duration in comparison to the population mean to 18 days[19]. According to our general pattern (Fig. 1) their total speed of migration decreased from 240 km/day (95% CrI: 196 – 296 km/d) to 183 km/day (95% CrI: 153 – 219 km/d) predicting a delayed arrival at the 8,700 km distant breeding areas of 11d (95% CrI: 8 – 15 d) tightly matching the field observations (7 – 16 d)[19].

Given that variation in total speed of migration is mostly determined by variation in total stop-over duration, we predict the range of advancement in spring arrival date by this mechanism specifically for songbirds. For this modelling we assumed that individual departure dates are rather inflexible[18,20] and ignored that they can be modulated by environmental conditions[21]. A 20% reduction in total stop-over duration would result in a two day advance in breeding area arrival for migration distances of 5,000 km, and seven days for 10,000 km (Fig. 2a; Supplementary Figure S1). To place these potential advances into an ecological context, consider that climate change has the largest advancing effect on primary consumers[22] and that time-series of caterpillar peak dates in European temperate forests (primary prey for nestlings of many songbird species) advanced by 20 d (UK, 1980-2008[23]), 15 d (Netherlands, 1985-2005[24]) and 9 d (Czech Republic, 1961-2007[25]). As most of the central and western European long-distance songbird migrants travel about 5,000-7,000 km, a 10 d advance would require a 50% reduction in total stop-over duration, and a 20 d advance would be unfeasible (Fig. 2a) through the predicted effect of total stop-over duration on total speed of migration (Fig. 1). Although these estimates demonstrate that individuals are highly unlikely to advance sufficiently by modifying migration speed alone, in reality it is even more difficult, because individuals can only anticipate environmental conditions when approaching their breeding grounds. Within the Palearctic-African migration system, this likely happens after crossing the Mediterranean Sea, i.e., on the final 1,000-3,000 km of their journey. According to our data, songbirds would migrate 3 d, 7 d, and 13 d for the last 1,000 km, 2,000 km, and 3,000 km, respectively. Reducing total stop-over duration by 50% only results in a 0.6 d, 1.8 d, and 3.1 d advance, respectively (Methods). Our analysis clearly demonstrates that the predicted phenotypic plasticity in the major component of migration speed, as estimated in the among-individual approach, is insufficient to keep up with the advancing spring of major breeding habitats.

Our predicted potential for adjusting arrival date can serve as a quantitative comparison for interpreting observed rates of advancement on the population level. In a dataset on arrival dates of the annual first 3-10 arriving males of ten trans-Saharan migrant species for 36-years (1981-2016) from Drenthe (NL, 52° 52 N, 6° 16' E)[3], arrival date trend varied between a delay of +2.6 d (95% CrI: -4.6 – +9.9 d) for spotted flycatchers (*Muscipata striata*), to an advance of –15.9 d (95% CrI: -21.1 – -10.7 d) in pied flycatchers (*Ficedula hypoleuca*) (Fig. 2b). These values were generally in the same order of magnitude as long-term changes in the migration phenology of UK breeding birds[5]. The most extreme observed advances in arrival (Fig. 2b) cannot be simply explained by a reduction in total stop-over duration and hence by maximizing total speed of migration due to favourable conditions en route (Fig. 2a). Alternatively, our among-individual comparison might not sufficiently well capture the true but unknown within-individual phenotypic plasticity. It seems, however, unlikely that the within-individual effect of reducing stop-over time on advancing arrival timing would be much stronger than predicted by our approach, because environmental conditions significantly affect stop-over duration[26]. The most likely candidate mechanism causing these earlier arrivals at the breeding areas is therefore a progressive advance in departure date from the wintering grounds[8]. This is supported by observations of pied flycatchers that have advanced spring passage through North-Africa by ca. 8d between 1970-2000[3] clearly demonstrating that advances have not solely been caused by speeding up migration at their final part of migration[27].

Climate change likely will continue to change phenologies at different rates[22], and here we have shown that long-distance migrant birds, with their relatively complex annual cycles, have limited capacities to flexibly adjust their migration phenology through modifying migration speed. This result could suggest that the observed strong advances in breeding area arrival in some species (Fig. 2b)[5] are caused by improving conditions prior to departure at the wintering grounds[21] resulting in an earlier spring departure timing through flexibility in

160 departure timing. Although we cannot rule out this mechanism, it is generally considered that
161 departure in long-distance migrants is triggered by photoperiod and hence not very
162 flexible[14,18,20]. Furthermore, conditions at wintering grounds often do not predict when
163 breeding grounds become profitable for arrival[3]. Alternatively, strong advances in breeding
164 area arrival are caused by an evolutionary response in spring departure timing[15]. In North
165 America, advances in spring arrival date across different species showed little plasticity
166 within individuals, and could not explain the population advance over the years, suggesting
167 ongoing evolutionary change although knowledge on heritability of arrival date was lacking[28].
168 Diurnal migrants that forage on the wing, e.g. swifts and swallows, have advanced their
169 arrival time stronger than nocturnal migrants in Britain[5]. This might not be caused by a
170 different evolutionary response, but possibly by a stronger phenotypic response to improving
171 foraging conditions en route yielding a stronger increase in rates of accumulating energy than
172 in nocturnal migrants. Evolution requires a genetic basis for variation in departure/arrival
173 dates and directional selection for an earlier arrival. The only system providing data on both
174 significant heritability and directional selection on arrival date concluded that the advance of
175 6 d in arrival over 20 years in great reed warbler (*Acrocephalus arundinaceus*) resulted from
176 phenotypic plasticity[9]. There are no other bird systems in which these mechanisms have
177 unequivocally been shown[10], let alone whether species differ in having e.g. enough genetic
178 variation in spring departure present in populations for evolution to operate. Our ability to
179 forecast the adaptive capacity of long-distance migrants to continuing global change requires
180 a much better understanding of why individuals within species differ in their annual timing,
181 but also why the responses to a changing environment differ considerably among-species
182 (Fig. 2b). To achieve this we need to better understand the (phenology of) trophic links during
183 breeding and especially including the conditions encountered at the wintering grounds.
184 Migrants are currently experiencing drastic environmental changes at their wintering grounds

that impact their survival[29], and these conditions likely have knock-on effects on later annual cycle stages[30] and hence these birds are in double jeopardy.

Methods

Methods, including statements of data availability and any associated accession codes and references, are available in the online version of this paper.

References

1. Walther, G.-R. *et al.* Ecological responses to recent climate change. *Nature* **416,** 389-395 (2002).
2. Visser, M. E. Keeping up with a warming world; assessing the rate of adaptation to climate change. *Proc. R. Soc. Lond. B* **275**, 649-659 (2008).
3. Both, C. Flexibility of timing of avian migration to climate change masked by environmental constraints en route. *Curr. Biol.* **20,** 1-6 (2010).
4. Møller, A. P., Rubolini, D. & Lehikoinen, E. Populations of migratory bird species that did not show a phenological response to climate change are declining. *P. Natl. Acad. Sci. USA* **105,** 16195-16200 (2008).
5. Newson, S. E. *et al.* Long-term changes in the migration phenology of UK breeding birds detected by large-scale citizen science recording schemes. *Ibis* **158,** 481-495 (2016).
6. Both, C., Bouwhuis, S., Lessells, C. M. & Visser, M. E. Climate change and population declines in a long-distance migratory bird. *Nature* **441,** 81-83 (2006).
7. Both, C. *et al.* Avian population consequences of climate change are most severe for long-distance migrants in seasonal habitats. *Proc. R. Soc. Lond. B* **277,** 1259-1266 (2010).
8. Knudsen, E. *et al.* Challenging claims in the study of migratory birds and climate change. *Biol. Rev.* **86,** 928-946 (2011).
9. Tarka, M., Hansson, B. & Hasselquist, D. Selection and evolutionary potential of spring arrival phenology in males and females of a migratory songbird. *J. Evol. Biol.* **28,** 1024-1038 (2015).
10. Charmantier, A. & Gienapp, P. Climate change and timing of avian breeding and migration: evolutionary versus plastic changes. *Evol. Appl.* **7,** 15-28 (2014).
11. Stephens, P. A. *et al.* Consistent response of bird populations to climate change on two continents. *Science* **352,** 84-87 (2016).
12. Saino, N. *et al.* Climate warming, ecological mismatch at arrival and population decline in migratory birds. *Proc. R. Soc. Lond. B: Biological Sciences* **278,** 835-842 (2011).
13. Sergio, F. *et al.* Individual improvements and selective mortality shape lifelong migratory performance. *Nature* **515,** 410-413 (2014).
14. Gwinner, E. Circadian and circannual programmes in avian migration. *J. Exp. Biol.* **199,** 39-48 (1996).
15. Jonzén, N. *et al.* Rapid advance of spring arrival dates in long-distance migratory birds. *Science* **312,** 1959-1961 (2006).
16. Alerstam, T. & Lindström, Å. in *Bird Migration: Physiology and Ecophysiology* (ed E. Gwinner) 331-351 (Springer, 1990).
17. Nilsson, C., Klaassen, R. H. G. & Alerstam, T. Differences in speed and duration of bird migration between spring and autumn. *Am. Nat.* **181,** 837-845 (2013).
18. Stanley, C. Q., MacPherson, M., Fraser, K. C., McKinnon, E. A. & Stutchbury, B. J. M. Repeat tracking of individual songbirds reveals consistent migration timing but flexibility in route. *PLoS ONE* **7,** e40688 (2012).
19. Tøttrup, A. P. *et al.* Drought in Africa caused delayed arrival of European songbirds. *Science* **338,** 1307 (2012).
20. Conklin, J. R., Battley, P. F. & Potter, M. A. Absolute consistency: Individual versus population variation in annual-cycle schedules of a long-distance migrant bird. *PLoS ONE* **8,** e54535 (2013).
21. Studds, C. E. & Marra, P. P. Rainfall-induced changes in food availability modify the spring departure programme of a migratory bird. *Proc. R. Soc. Lond. B* **278,** 3437-3443 (2011).

22. Thackeray, S. J. *et al.* Phenological sensitivity to climate across taxa and trophic levels. *Nature* **535,** 241-245 (2016).
23. Charmantier, A. *et al.* Adaptive phenotypic plasticity in response to climate change in a wild bird population. *Science* **320,** 800-803 (2008).
24. Both, C., van Asch, M., Bijlsma, R. G., van den Burg, A. B. & Visser, M. E. Climate change and unequal phenological changes across four trophic levels: constraints or adaptations? *J Anim. Ecol.* **78**, 73 - 83 (2009).
25. Bauer, Z. *et al.* Changing climate and the phenological response of great tit and collared flycatcher populations in floodplain forest ecosystems in Central Europe. *Int. J. Biometeorol.* **54,** 99-111 (2010).
26. Deppe, J. L. *et al.* Fat, weather, and date affect migratory songbirds' departure decisions, routes, and time it takes to cross the Gulf of Mexico. *P. Natl. Acad. Sci. USA* **112,** E6331-E6338 (2015).
27. Jonzén, N., Hedenström, A. & Lundberg, P. Climate change and the optimal arrival of migratory birds. *Proc. R. Soc. Lond. B* **274,** 269-274 (2007).
28. Van Buskirk, J., Mulvihill, R. S. & Leberman, R. C. Phenotypic plasticity alone cannot explain climate-induced change in avian migration timing. *Ecol. Evol.* **2**, 2430-2437 (2012).
29. Zwarts, L., Bijlsma, R. G., van der Kamp, J. & Wymenga, E. *Living on the edge: Wetlands and birds in a changing Sahel*. (KNNV Uitgeverij, 2009).
30. Harrison, X. A., Blount, A. D., Inger, R., Norris, D. R. & Bearhop, S. Carry-over effects as drivers of fitness differences in animals. *J. Anim. Ecol.* **80**, 4-18 (2011).

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Author contribution

H.S. designed the study. H.S. analysed the tracking data and modelled the phenotypic response. C.B. analysed the phenology data. H.S. and C.B. wrote the paper.

Additional Information

Supplementary information is available in the online version of the paper. Reprints and permissions information is available online at www.nature.com/reprints. Publisher's note: Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations. Correspondence and requests for materials should be addressed to H.S.

Competing financial interests

The authors declare no competing financial interests.

Figure 1 | Total stop-over duration explains variation in total speed of migration in seven taxonomic bird groups. a, Individual total speed of migration plotted against individual total stop-over duration for seven taxonomic bird groups in spring (geese: dark blue, storks: grey, raptors: orange, waders: light blue, gulls: green, swifts: yellow, and songbirds: purple). Total stop-over duration and bird group explained 66% of variation in total migration speed (Methods). **b**, 95% credible intervals (CrI) of the estimated intercept, β_0, and **c**,) of the slope, β_1, for the bird group-specific regressions. **d**, 95% CrI of total number of stop-over days for a 1,000 km long migratory journey. Sample size per bird group is given in **b**.

Figure 2 | Change in (a) predicted total duration of migration as a function of a change in total stop-over duration in migratory songbirds, (b) arrival dates of ten migratory birds between 1982-2016 (NL). a, The average total duration of migration was estimated for different migration distances based on the songbird-specific total number of stop-over days with 3.2 days per 1,000 km (Fig. 1d). Predicted changes in total migration duration were calculated based on the mechanism of how a change in total stop-over duration affects total speed of migration. Contour lines clarified these changes in steps of 5 d intervals. Numbers given in the middle of the figure indicate total duration of migration in days for a given migration distance, e.g. arrows point out total duration of migration for 14,000 km. **b**, Each year between 1981-2016 arrival of the first 10 males (filled circle) or the first 3 males (open circles) were scored by the same observer in a restricted area in Drenthe (NL). Species specific estimates are the linear slopes of the annual mean against year, multiplied by 35 years and ordered from strongest advancements towards delays. Mean slopes, corresponding 95% credible intervals, and number of considered years are given.

Methods

Total speed of migration and total stop-over duration. We considered individual tracking data of 49 migration studies (Supplementary Tables S1, S2). Detailed information about total migration distance, total duration of migration, and total stop-over duration for spring migration were given on individual level for 320 birds (Supplementary Tables S1, S2). Total speed of migration was individually estimated as the individual total duration of migration divided by the corresponding total migration distance. All values were considered as provided in the original publications. There are obviously differences in how stop-overs were defined and in how accurate total migration distances were estimated, e.g. global positioning system data vs. light-level geolocation data[31] and accurately determined migration distance vs. great circle distance between wintering ground and breeding area. We did not correct for these general differences in data quality. As still a high proportion of the variation (66%) in total speed of migration was explained by total stop-over duration and bird group (Fig. 1), we are convinced that if data quality were less variable, the dependence of total speed of migration on total stop-over duration and bird group would be even stronger.

Statistics were calculated using the statistical software R 3.2.1[32]. We applied a Bayesian approach to analyse the data[33]. Variation in total speed of migration was modelled using a linear mixed effect model. Total stop-over duration and bird group were used as explanatory variables. Their two-way interaction was considered to estimate bird group-specific regressions. Total number of stop-over days and total speed of migration were both log10-transformed to obtain a linear relationship between these parameters. As a few individual birds did not perform a single stop-over day during their migration, i.e., their total stop-over duration was zero, we added the 6^{th} quantile of all individual total stop-over durations which is 1.14 (days) to that value before transformation. Field study was included as a random factor to account for repeated measures of the same species within the same study. We allowed for

both random intercepts and random slopes in the linear mixed effect model, i.e., an own intercept and slope were permitted for each field study. Diagnostic residual and random effect plots did not show deviation from the model assumptions. We used improper prior distributions, namely $p(\beta) \sim 1$ for the coefficients, and $p(\beta) \sim 1/\sigma$ for the variance parameters. To obtain the posterior distribution we directly simulated 2,000 values from the joint posterior distribution of the model parameters using the function sim of the package "arm"[34]. The medians of the simulated values from the joint posterior distributions of the model parameters were used as estimates, and the 2.5% and 97.5% quantiles as lower and upper limits of the 95% credible intervals (CrI). The corresponding values are given in Figure 1 and Supplementary Table S3. 66% of variance was explained by the fixed factors total stop-over duration and bird group. 93% of variance was explained by the entire model, i.e., by both fixed and random factors[35]. Considering the variation of the specific $\beta_{0,i}$- and $\beta_{1,i}$-values (Fig. 1b,c), there is a bird group-specific$_{[i]}$ mechanism of how total stop-over duration affects total speed of migration:

$$Total\ speed\ of\ migration_i = 10^{(\beta_{0,i} + \beta_{1,i} * log10(total\ stopover\ duration_i))} \quad \text{eqn. (1).}$$

Number of stop-over days per migration distance. The number of total stop-over days per 1,000 km of migration was calculated as the log10-transformed total stop-over duration divided by total migration distance and multiplied by 1,000. Variation in number of total stop-over days per 1,000 km was modelled using a linear mixed effect model. Bird group was used as an explanatory variable. Field study was included as a random factor. Here we could allow only for random intercepts in the linear mixed effect model, but not for random slopes. Diagnostic residual and random effect plots did not show deviation from the model assumptions. Estimates and 95% CrI were calculated as described above.

Change in predicted total duration of migration as a function of a change in total stop-over duration for songbird migrants. Based on the data provided by the tracking studies of songbirds and our calculations, songbirds perform 3.2 d (95% CrI: 2.3 – 4.8 d) of stop-over per 1,000 km (Fig. 1d). First, we calculated the total number of stop-over days for a migration range of 5,000 km assuming 3.2 stop-over days per 1,000 km of migration, i.e. 16 d. For this 5,000 km migration range we let then vary the total stop-over duration from -50% to +50% in steps of 1%. We incorporated these 101 different estimates of total stop-over durations into eqn. 1 with the songbird-specific estimates for the intercept and the slope (Fig. 1b,c and eqn. 1) to model the corresponding 101 different total speeds of migration. By dividing the migration range of 5,000 km by these values we received 101 different estimates of total duration of migration based in the 101 different total speeds of migration. Finally, these 101 estimates of total duration of migration were related to the original (not changed) estimate of total duration of migration, i.e. the 51st value. Thus, decreasing the total stop-over duration resulted in a shorter total duration of migration and increasing the total stop-over duration resulted in a longer total duration of migration (Fig. 2a). This procedure was repeated for different migration ranges increasing in steps of 100 km to the maximum migration range of 15,000 km considered here. The graphical solution of this modelling is given in Figure 2a and Supplementary Figure S1. We modelled the effect of a change in total stop-over duration in the same way also for the lower (Supplementary Figure S1a) and the upper limit of the 95% CrI (Supplementary Figure S1c) for the estimated average number of stop-over days per 1,000 km (Fig. 1d). The graphical solutions of these modelling are given in Supplementary Figure S1.

Arrival dates of 10 migratory birds between 1982 – 2016. Every year between 1981 – 2016 the first arriving three to ten males were recorded by the same observer, Rob G. Bijlsma, of all migrant species that do not winter in the area, and breed in the forests of Drenthe (northern

Netherlands, 6° 17’ E, 52° 52’ N)[7]. The area was visited on a daily basis during spring and summer (from late February onwards). Individuals that were recorded once were not counted as new arrivals the next day, so data are from separate individuals within a year. The study area is forested with conifers and interspersed with heaths and deciduous woodland. Arrival dates of males was monitored by observing singing birds, and given the intensity of the observer’s presence, are probably accurate[7]. For instance, when birds were seen before any song was heard, singing was almost always recorded later the same day. Sample size differences between species in number of individuals per year depend on their general abundance. From the abundant species the first ten individuals were recorded, whereas from other species the first three individuals were recorded as indicated in Figure 2b. Variation in arrival date was modelled for each species separately by a simple linear regression. Julian day of the tenth or third recorded individual was used as the explanatory variable. Diagnostic residual plots did not show deviation from the model assumptions. The species-specific median of the simulated values from the joint posterior distribution of the model parameter was used as the estimated slope, and the 2.5% and 97.5% quantiles as lower and upper limits of the 95% credible intervals (CrI).

Trends in first arrival dates can be affected by population trends, because as in declining populations fewer individuals will be in the early tail, whereas in growing populations more individuals will be in the early tail. We checked for this possible artefact by considering population trends as observed in a forest area (Dwingelderveld, 6° 24’ E, 52° 48’ N) of similar habitat ca. 10 km south-east of the area from where the phenological observations were made (Fig. 2b). Each year, Joop Kleine counted breeding birds by territory mapping in Dwindelderveld. Here we considered his data from 1987-2016 for the same set of species as incorporated in our phenological observations (Fig. 2b). For each of the ten species, we calculated the population trend as the slope of log10-transformed population size to year. Four species showed a significant population decline, three a significant increase, and three no

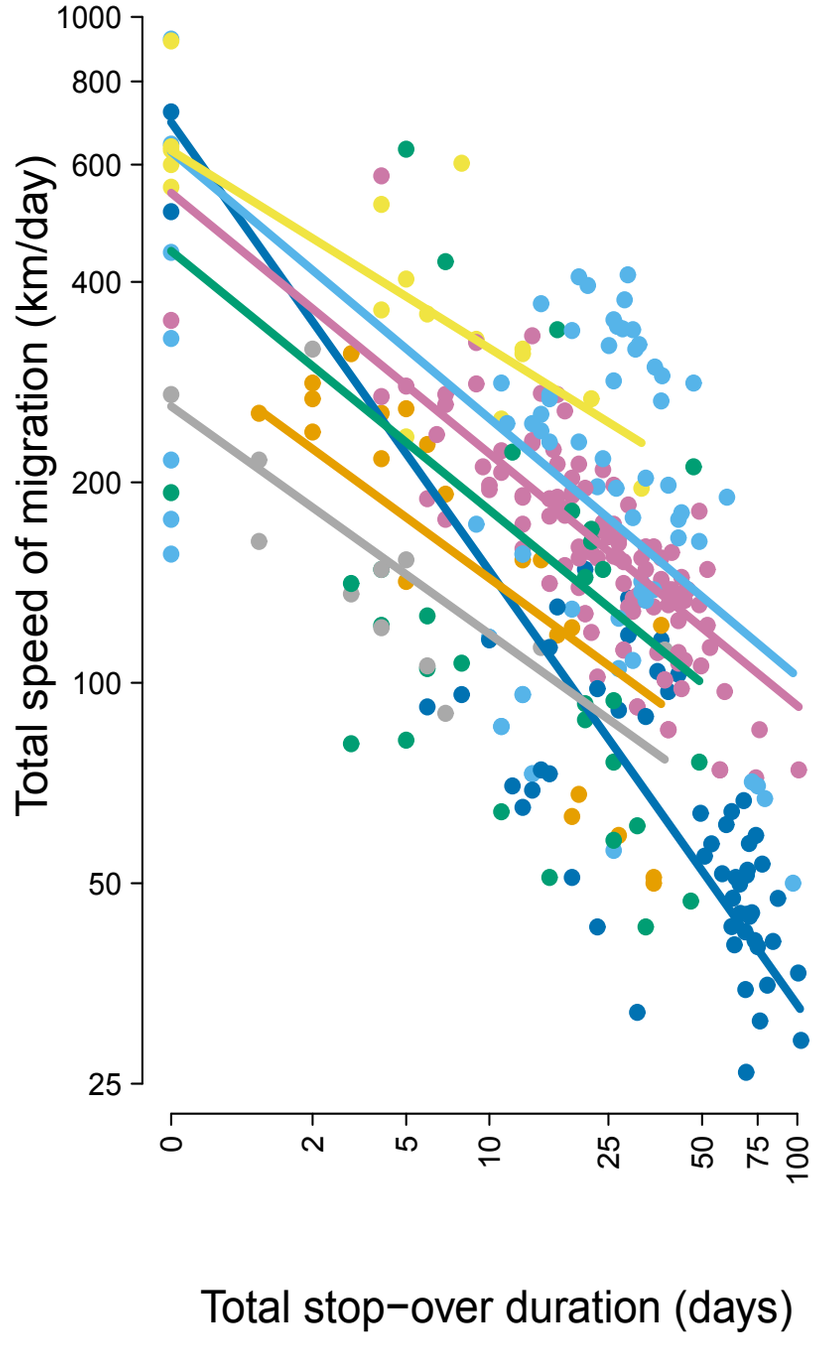
significant change over the years. We found no correlation between local population trend (1991-2011) and the trend in phenology (1982-2016, Fig. 2b; Pearson correlation: r = -0.12, N = 10, p = 0.74). The strongest advancements in arrival were observed in a species with declining population size (common cuckoo), a species without a trend (wood warbler) and an increasing species (pied flycatcher). Therefore, we feel rather confident that the variation in arrival trend, as observed between species in Figure 2b, is not a matter of changes in their abundance.

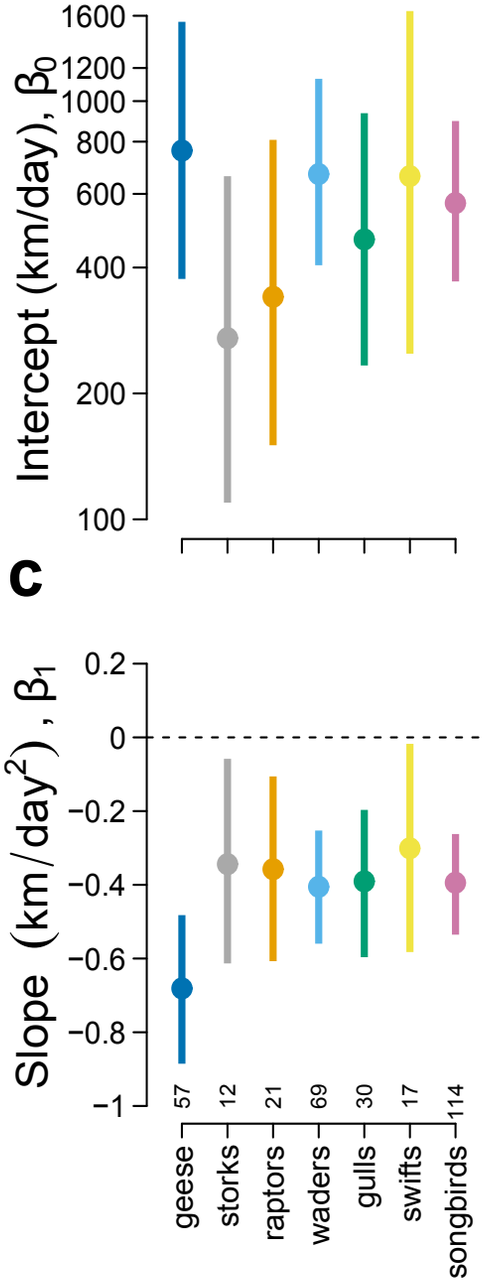
Data availability: The authors declare that the data supporting the findings of the total speed of migration and total stop-over duration analysis are available within the article's supplementary information files. The data that support the findings of the arrival date analysis are available from C.B. upon request.

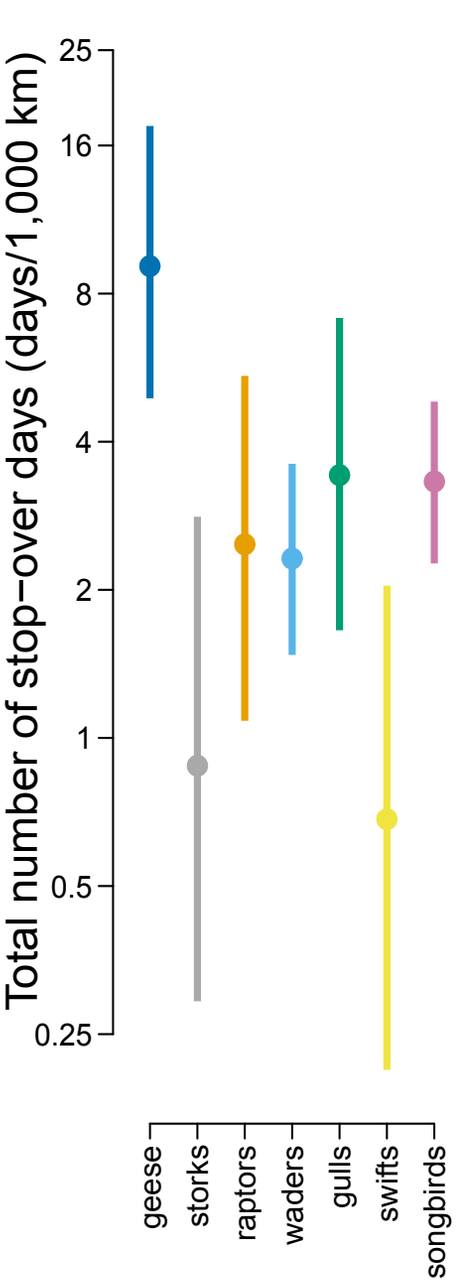
Code availability: R code for modelling will be shared upon request, please address H.S. (heiko.schmaljohann@ifv-vogelwarte.de).

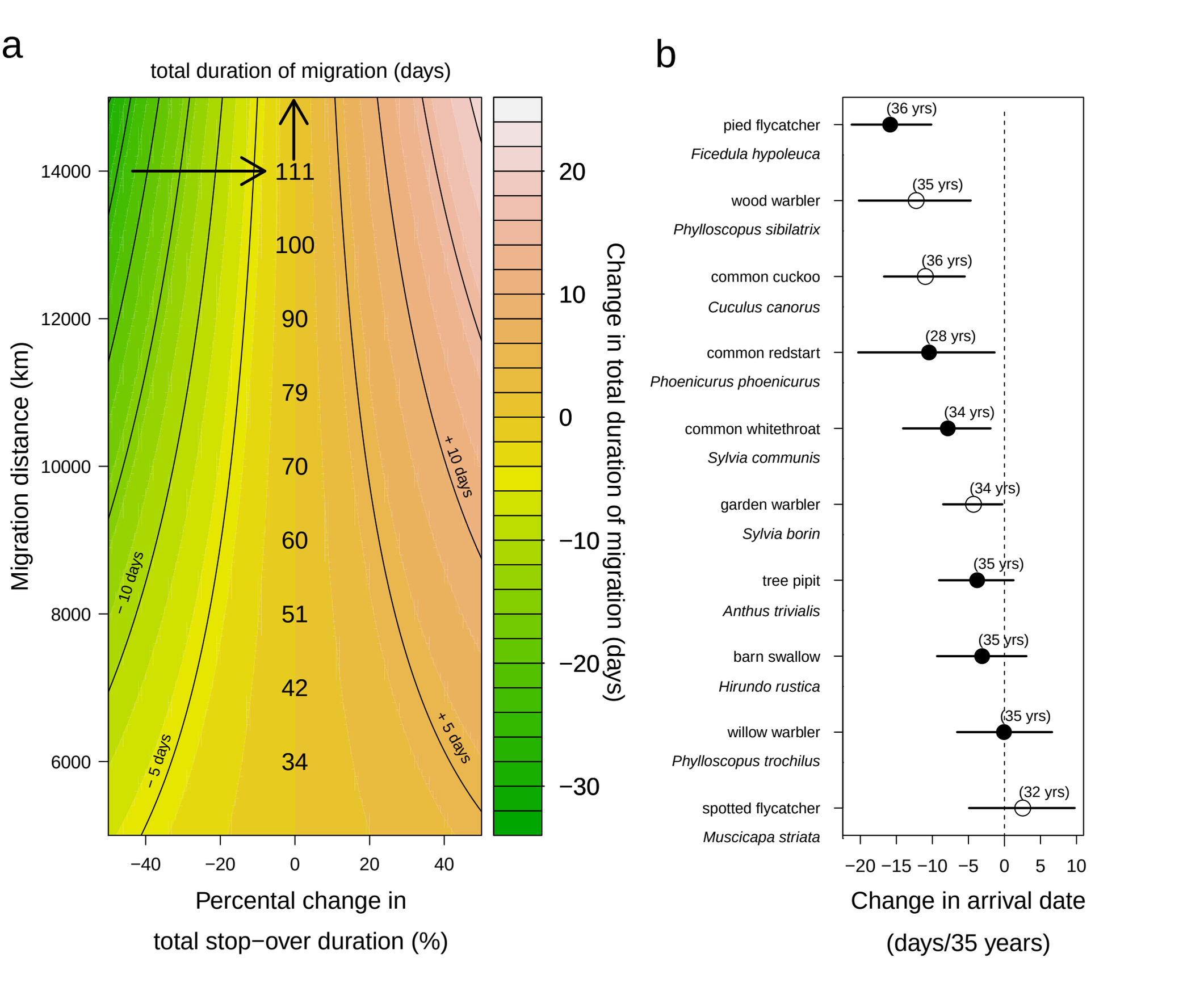
References

31. Rakhimberdiev, E. *et al.* Comparing inferences of solar geolocation data against high-precision GPS data: annual movements of a double-tagged black-tailed godwit. *J. Avian Biol.* **47,** 589-596 (2016).
32. R Core Team. R: A language and environment for statistical computing. (2015).
33. Korner-Nievergelt, F. *et al. Bayesian data analysis in ecology using linear models with R, BUGS, and Stan*. (Elsevier, 2015).
34. Gelman, A. & Hill, J. *Data analysis using regression and multilevel/hierarchical models*. (Cambridge University Press, 2007).
35. Johnson, P. C. D. Extension Nakagawa & Schielzeth's R^{2GLMM} to random slopes models. *Method. Ecol. Evol.* **5,** 944-946 (2014).


a
Total speed of migration (km/day)
1000
800
600
400
200
100
50
25
0
2
5
10
25
50
75
100
Total stop−over duration (days)


b
Intercept (km/day), β_0
1600
1200
1000
800
600
400
200
100
c
Slope (km/day^2), β_1
0.2
0
−0.2
−0.4
−0.6
−0.8
−1
57
12
21
69
30
17
114
geese
storks
raptors
waders
gulls
swifts
songbirds
Bird group


d
Total number of stop−over days (days/1,000 km)
25
16
8
4
2
1
0.5
0.25
geese
storks
raptors
waders
gulls
swifts
songbirds
Bird group


a
total duration of migration (days)
Migration distance (km)
14000
12000
10000
8000
6000
111
100
90
79
70
60
51
42
34
+ 10 days
− 10 days
+ 5 days
− 5 days
−40
−20
0
20
40
Percental change in
total stop−over duration (%)
Change in total duration of migration (days)
20
10
0
−10
−20
−30
b
pied flycatcher
Ficedula hypoleuca
(36 yrs)
wood warbler
Phylloscopus sibilatrix
(35 yrs)
common cuckoo
Cuculus canorus
(36 yrs)
common redstart
Phoenicurus phoenicurus
(28 yrs)
common whitethroat
Sylvia communis
(34 yrs)
garden warbler
Sylvia borin
(34 yrs)
tree pipit
Anthus trivialis
(35 yrs)
barn swallow
Hirundo rustica
(35 yrs)
willow warbler
Phylloscopus trochilus
(35 yrs)
spotted flycatcher
Muscicapa striata
(32 yrs)
−20 −15 −10 −5 0 5 10
Change in arrival date
(days/35 years)